Simulation of geographical trends in Chowdhury ecosystem model

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Abstract: A computer simulation based on individual births and deaths gives a biodiversity increasing from cold to warm climates, in agreement with reality. Complexity of foodwebs increases with time and at a higher rate at low latitudes, and there is a higher rate of species creation at low latitudes. Keeping many niches empty makes the results correspond more closely to natural gradients.

1 Introduction

Chowdhury et al [1] have proposed a model, recently reviewed in [2, 3], that aims to model microevolution (at the level of populations over ecological time) and macroevolution (at the level of species and above, over geological time). So far, geographical trends have not been included in the model. However, evolution is not uniform across all habitats and regions, but shows distinct geographical trends. Most distinct and best studied are latitudinal gradients in species diversity, i.e., an increase in species numbers from high to low latitudes, e.g. from the Arctic to the Amazonas. A realistic model must take such gradients into account, and the possibility of incorporating gradients can indeed be used as a test for the usefulness of the model.

Whereas evidence for latitudinal gradients is convincing, empirical evidence for greater productivity at low latitudes is equivocal. We examine this question using animal numbers as rough indicators of productivity.

Furthermore, fossil data indicate that diversity has increased over geological time, e.g., [4], and ecosystems of different age differ distinctly in diversity. Thus, the Indo-Pacific Ocean is much older (as old as oceans themselves, i.e.

many hundred million years) than the Atlantic which began to form only about 150 million years ago. Diversity of teleost fish and many other groups is much greater in the former. Also, although latitudinal gradients are found in both oceans, they are much more distinct in the Indo-Pacific [5]. A further test for the validity of a model would therefore be whether such differences can be quantitatively reproduced by it.

Rohde [6, 7] has suggested that latitudinal gradients in diversity arise as the result of faster evolutionary rates at high temperatures. One implication of this hypothesis is that new species, many with great complexity, arise predominantly in the tropics, from where they spread into higher latitudes (also [8]). Moreover, taxa with little dispersal/vagility should have steeper gradients than those with great dispersal/vagility.

We adapt the parameters in the model to test the following: 1) species numbers decrease from low to high latitudes at rates corresponding to empirical data; 2) complexity of ecosystems, as indicated by the number of trophic levels, increases over evolutionary time and at a higher rate in the tropics; 3) new species arise predominantly at low latitudes, 4) there is an increase of productivity (indicated by total animal numbers) from high to low latitudes; 5) diversity gradients for taxa that diffuse slowly are steeper than those for taxa that diffuse more rapidly into higher latitudes.

2   Model and Results

The Chowdhury model [1, 2, 3] simulates the birth, ageing and death of individual animals. The minimum reproduction age, number of offspring per birth, the prey-predator relations and the number of food levels self-organize, with a new food level added if the total number of animals is not too large. Also mutation, speciation, and migration on a square lattice are included. We refer to recent reviews [2, 3] for details and a discussion of similar but simpler models, and to [9] for a systematic study of the dependence on various parameters. The present simulations used a 4×4 lattice, up to 10^8 time steps for each animal, and up to 10 food levels; food level ℓ allowed for up to $2^{\ell-1}$ different species. If not given below otherwise, the mutation rate was $p_{mut} = 0.01$, while the carrying capacity n_{max} (maximum number of animals per species and per lattice site) was 100.

Now we interpret the four lines of the lattice as cold, temperate, subtropic and tropic latitudes, and assume the probability to give birth as proportional
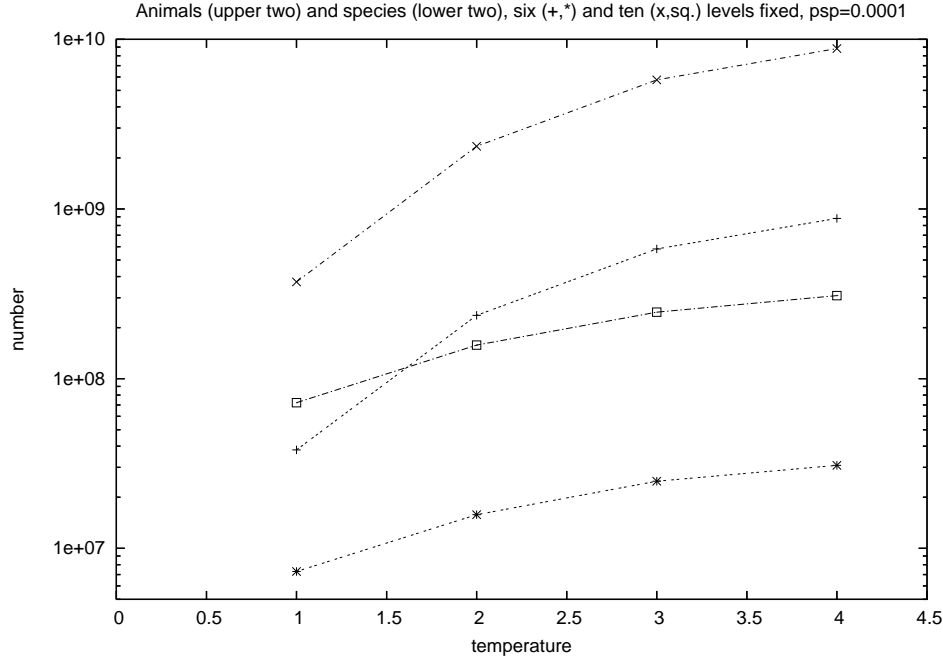
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Figure 1: Summed numbers of animals (+ and x) and species (stars and squares) in 20 million iterations, versus temperature (= line number in 4×4 lattice).

to the line number. Thus in the tropics this probability is four times higher than in the cold regions. In the plots below we denote the line number as temperature. Births in the Chowdhury model are offspring surviving until their mortality becomes independent of age (below the minimum reproduction age).

When this model was simulated for speciation rate $p_{sp} = 0.1$, the number of animals increased and the number of species decreased for increasing temperature. This does not correspond to what is usually found in nature. Then we omitted migration and kept the number of food levels fixed at six (or at ten), thus finding a slight increase of the number of species, much weaker than the increase for the number of animals. Finally we reduced p_{sp} from 0.1 to 0.0001, and found the desired strong increase in the numbers of both animals and species, Fig.1. The variation with speciation probability is shown in Fig.2; we see that it does not affect the temperature dependence of
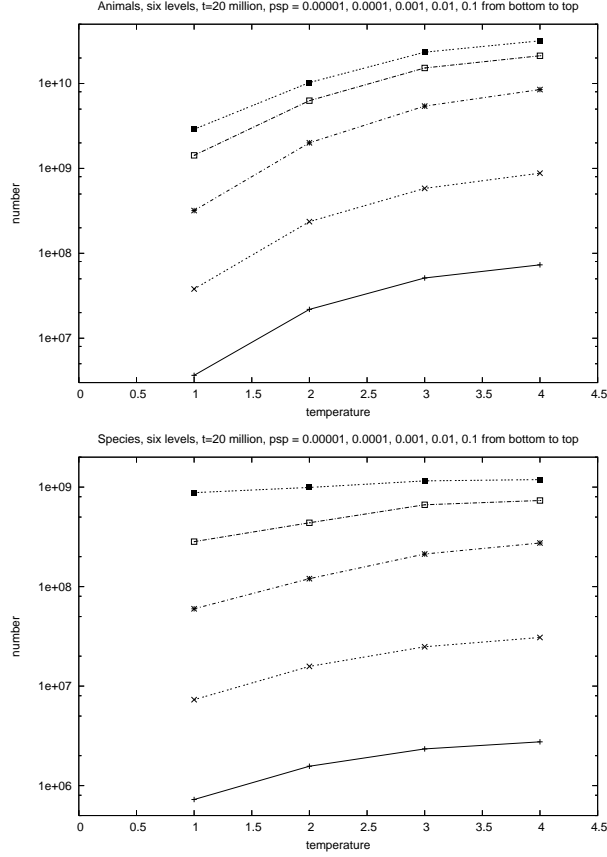
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Figure 2: Summed number of animals (part a) and species (part b) for speciation probabiltiy $10^{-5} \ldots 10^{-1}$ increasing from bottom to top.

the animal numbers, but strongly affects that of the species numbers. Only for low speciation probabilities, when ecological niches left empty by an extinct species stay empty for a long time, do we see a strong temperature dependence also for the species numbers. The dependence on p_{mut} is shown in Fig.3, that on $n_{max} = 100 \ldots 10000$ is not shown since the species numbers barely change.

In the above results, no migration was allowed. Including diffusion to neighbouring empty lattice sites makes it easier to refill ecological niches after extinctions and reduces the temperature dependence of the species numbers, similar to the variation with p_{sp} in Fig.2. Fig.4 shows this effect for the case
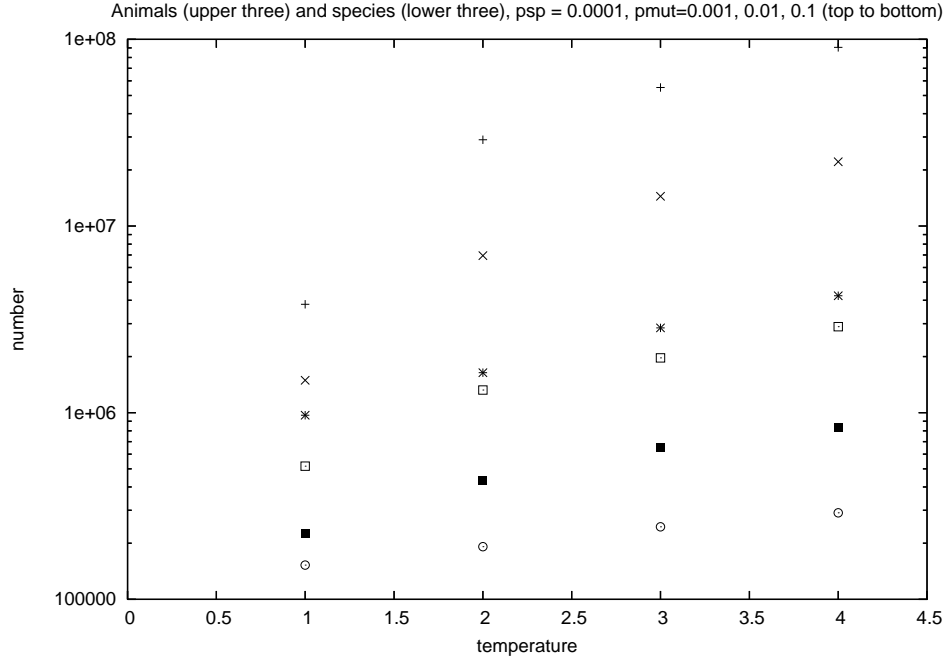
Figure 3: Summed animal numbers (upper data) and species numbers (lower data) for mutation probability 0.1, 0.01, and 0.001 (from top to bottom); $p_{sp} = 0.0001$.

that the diffusion is proportional to the line number, i.e. our times higher in the tropical than in cold climates, and in the tropics increases from 0 to 0.5 from bottom to top in Fig.4. Fig.5 shows the species numbers if the diffusivity, instead of depending on the geographical latitude as in Fig.4, is proportional to the height of the food level. Thus the big predators on the top of the food web move more than the prey on the bottom. Instead of summing up over all levels, this Fig.5 shows the numbers in the various levels. The number of top predators now depends slightly less on temperature than that of the bottom prey.

Until now we kept the numbers of food levels fixed, as in some earlier versions of the Chowdhury model; otherwise, as mentioned above we found a decrease of species number with increasing temperature. If we allow a new food level to be added, with probability 0.1, if the total number of animals on the lattice site is greater (and not smaller as before) than n_{max}, then we get
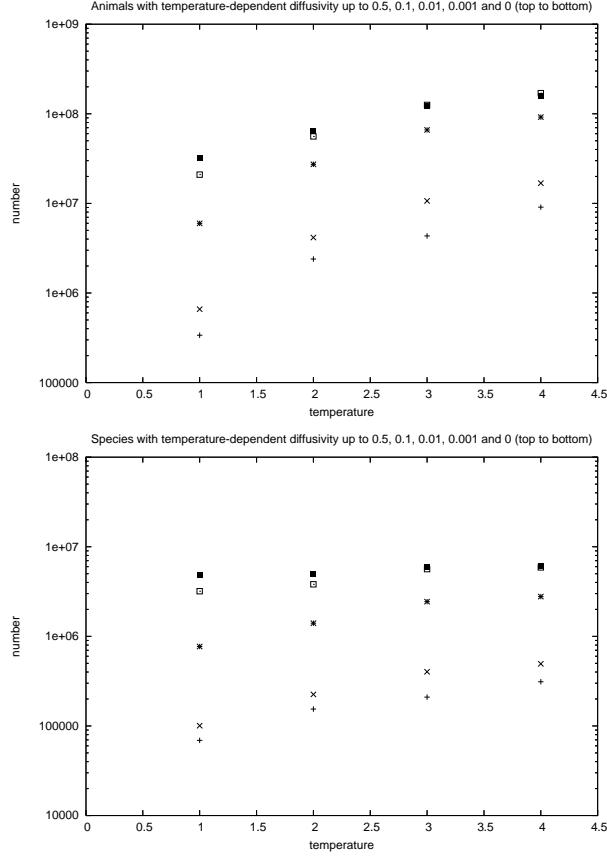
Figure 4: Effect of diffusion for animals (part a) and species (part b).

species numbers increasing with temperature, similar to Fig.1 (not shown). Fig.6 shows the dependence of the number of levels on time, and Fig. 7 on temperature. The number of levels soon reaches the maximum of ten which the program does not allow to exceed. Migration was not allowed. (We start with 3 levels and do not allow more than 10 levels, as symbolized by the horizontal lines in Figs. 6 and 7.)

For this case of increasing numbers of food levels and relatively short time spans, a constant strong probability 1/2 of migrating to a neighbouring empty niche gave a rapid increase of species numbers with temperature from cold to temperate (1 to 2) latitudes, followed by a slight increase to warmer latitudes, as illustrated in Fig. 8.
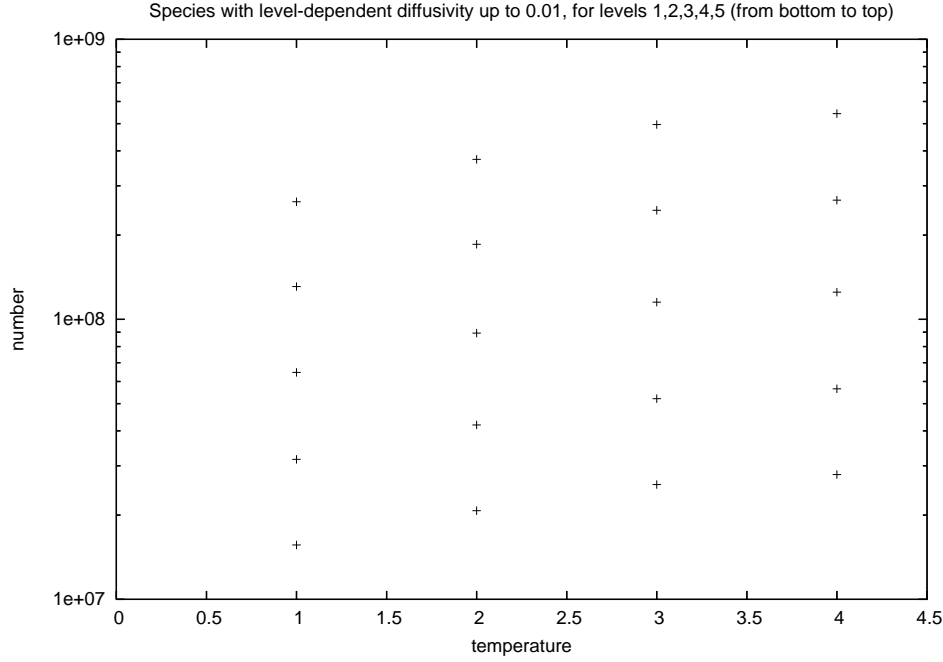
Figure 5: Summed species numbers, for five of the six simulated levels, when the diffusivity is 0.01 for the top food level and decreases linearly with increasing level number to zero at level six. The low levels correspond to the large numbers; the top level contains at most one species at a time.

3 Discussion

The two major aspects examined in this paper are latitudinal gradients in *species* numbers and in productivity, the latter measured as *animal* numbers.

Latitudinal gradients in species diversity, i.e., an (often very great) increase in species numbers from high to low latitudes, are the most distinct and best studied geographical trends. There are exceptions, but most groups of animals and plants are much richer in the tropics than in temperate and cold climates, as reviewed in [6, 10, 11]. For example, the shallow waters of the Philippines have about 2000 fish species, South Australia has about 300, and the Antarctic/Subantarctic Ocean less than 100 (further details and references in [12]). Fossil evidence suggests that latitudinal diversity gradients have existed for at least 270 million years [13] or may even be time invariant
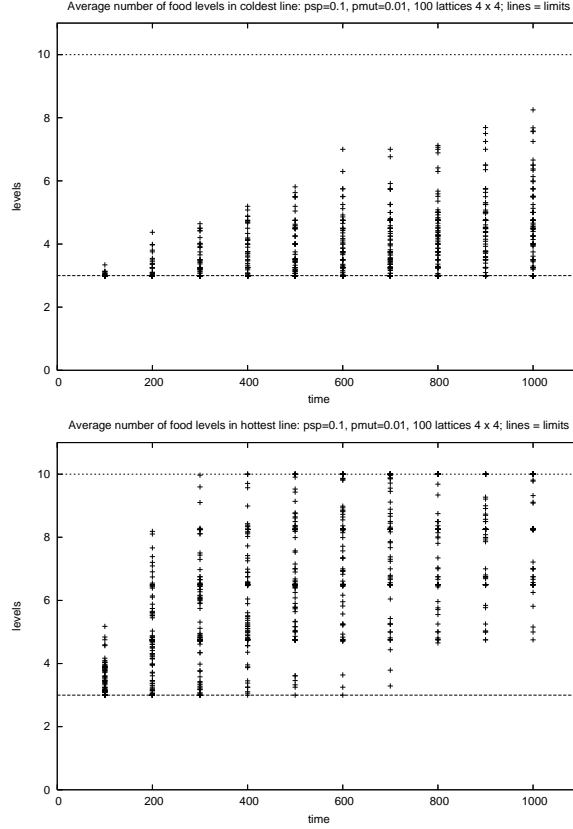
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Figure 6: Time development in the number of food levels for the coldest (part a) and the hottest (part b) region. For 10 time intervals of 100 iterations each, we show each of hundred samples, but the symbols may overlap.

[14].

The relationship between productivity and latitudinal gradients is by no means clear. For example, the Antarctic/Subantarctic Ocean is highly productive , as indicated for example by its huge quantities of krill, the staple food of many whales. On the other hand, most tropical seas do not have particularly high productivity but are very rich in species, although coral reefs are both species rich and productive. The mean production in the open ocean in gram of carbon per square meter, is 50 per year, that in the coastal zone 100 per year, whereas a coral reef had a production of about 3500 per year (for details and references see [15]). According to [16], who evaluated
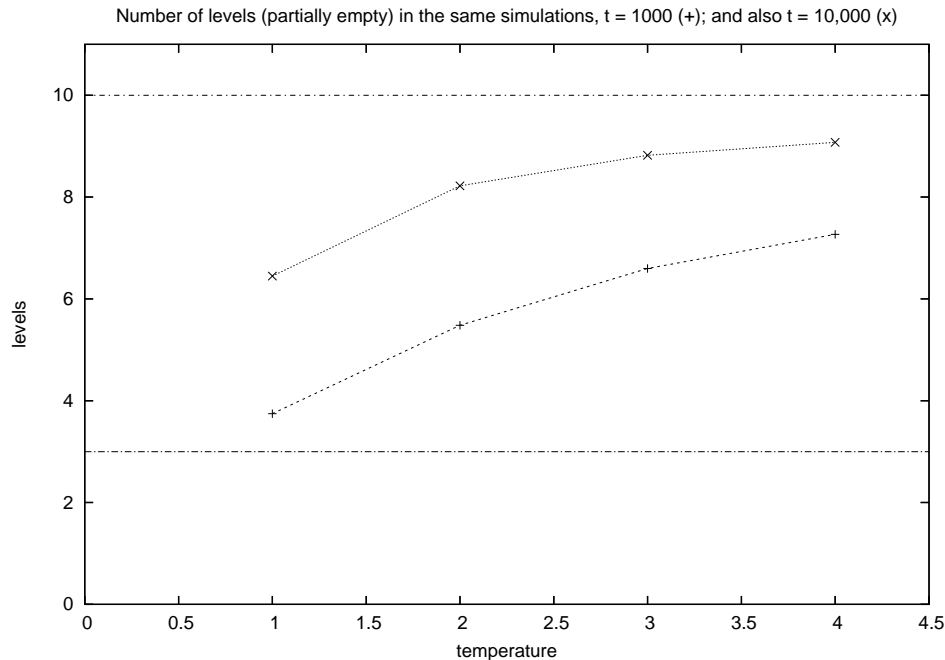
Figure 7: From the simulations in Fig.6 and additional ones up to $t = 10^4$, we show the temperature dependence of the average number of levels.

data from many studies, the relationship between diversity and productivity depends on scale. In this study we are concerned with continental/global, and with regional scales. At the former (more than 4000 km), unimodal or positive relationships are frequently found, although absence of or negative correlations occur as well. At the latter (200-4000 km) absence of or negative correlations are approximately as common as unimodal or positive relationships for plants, and slightly more common for animals.

Among the best known systems are freshwater ones. Approximately 40% of fish species and almost 20% of all vertebrates occur in freshwater (p. 126 in [17]). With regard to freshwater lakes, most species of fish are found in some large African tropical lakes. Lakes Victoria, Tanganyika and Malawi (121, 500 km^2) have a total of about 1,450 freshwater fish species (17% of the Earth's total) ([17], p. 127). Lake Malawi (28, 231 km^2) alone contains 550 or more species. In contrast, the cold-temperate large lakes in the northern hemisphere are much poorer. Thus, only 173 fish species are found in
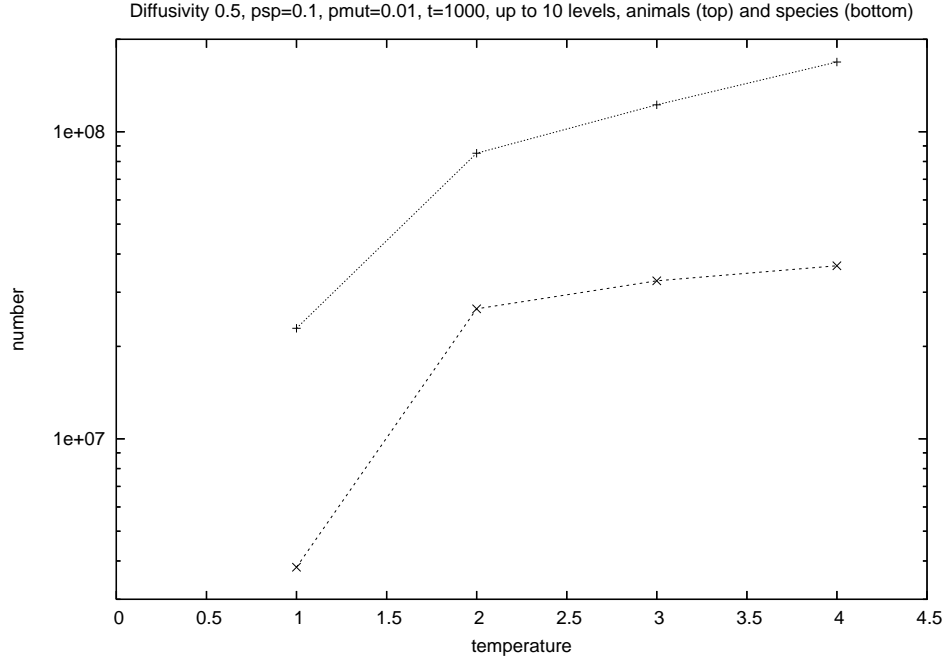
Figure 8: Simulations as in Fig.7 but with diffusivity 1/2 instead of zero.

the North American Great Lakes (246, 900 km^2) ([17], p. 127), and Lake Baikal has 39 (Sheremetyev, personal communication), and this in spite of the North American Great Lakes and Lake Baikal together containing 31% of the Earth's freshwater. The poor fauna cannot be due to glaciations. The high endemicity of its fauna indicates that Lake Baikal was little affected by them during the Ice Ages.

Productivity is generally higher in low than in high latitude lakes, with much overlap. Net primary productivity, measured in gram of carbon per square meter, of tropical lakes ranges from 0.100 to 7.6 per day, and from 30 to 2500 per year. In temperate lakes it ranges from 0.005 to 3.6 per day, and from 2 to 950 per year ([18], p. 192). Annual productivity in the North American Great Lakes is ca. 100 to 310 ([19], Table 14-10), or 80-90 to 240-250 ([18], pp. 194-195); in Lake Baikal it is 122.5 ([18], p. 194). In contrast, Lake Victoria, has an annual production of 640 ([19], Table 14-10), among the highest for freshwater lakes. Evidence is strong that the highest diversity of freshwater fishes is found in tropical, highly productive lakes.

The correlation between species diversity and productivity may often be complicated by geographical and/or historical contingencies (such as upwellings in oceans that carry inorganic substances to the surface resulting in increased productivity). Such contingencies cannot be considered in general evolutionary/ecological models, such as the Chowdhury model. However, experimental evidence suggests that there should indeed be an increase in productivity (measured as animal numbers in the model) with diversity, even if all other conditions are equal. Experimentally increasing biodiversity by a factor of two or three increased productivity by the same factor [20]. Experimental studies reviewed in [21] also showed that greater species diversity increases productivity. These studies provide evidence that primary productivity can be positively correlated with plant species richness for two reasons, differences between species in richer systems may allow complementary use of resources, and there is a higher probability of containing highly productive species in richer systems.

In summary, we return to the 5 aims stated at the end of the Introduction: 1) An increase of species numbers with temperature is reproduced in Figs. 1 to 5. 2) Figs. 6 and 7 show that the complexity of the foodwebs increases with time and at a higher rate in the tropics. 3) Since we did not allow for migration in Figs. 1 to 3, the increase of species with increasing temperature means also a higher creation rate of species in warmer climates. 4) Also the animal numbers increased, usually even stronger that the species number, with increasing temperature. 5) The biodiversity gradient for fast-moving predators is lower than that for slow-moving prey, but only slightly.

Therefore the simulations, qualitatively at least but to some degree (as far as is possible in view of the great variability of natural gradients) also quantitatively, agree with our aims.

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